

A NEW DEVONIAN OPHIUROID  
(ECHINODERMATA: OEGOPHIURIDA) FROM  
NEW YORK STATE AND ITS BEARING ON THE  
ORIGIN OF OPHIUROID UPPER ARM PLATES

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*Abstract.*—The genus *Strataster* Kesling and Le Vasseur, 1971, [Protasteriidae] is revised, and *S. maciverorum*, a new species, is reported from the Panther Mountain Formation (Middle Devonian) near Cooperstown, New York. All of the species of *Strataster* (amended) have upper arm plates; those of *S. maciverorum* resemble the carinal plates of starfish. The prevailing view that upper arm plates are absent in the Oegophiurida is abandoned. The arrangement of the alternating ambulacral plates in *Strataster* is identical to the arrangement in echinoids, and the madreporite is located in interradius III/IV of Lovén's system. These findings necessitate a revised diagnosis of the Oegophiurida. The new data also clarify the history of the upper arm plates of modern ophiuroids. These plates are serially homologous with the primary radial plates of the ophiuroid calycinal system. Ophiuroid arm segmentation was perfected after upper arm plates were brought into serial correspondence with the ambulacral vertebrae.

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The Devonian ophiuroids of New York State continue to provide important material for the investigation of questions at the higher levels of echinoderm classification. Ophiuroid fossils collected by Dr. Monroe A. McIver and Elizabeth P. McIver of Cooperstown, New York, and donated to the New York State Museum are described here as *Strataster maciverorum*, new species. The starfish-like aboral appearance of these specimens was, for a long time, an impediment to their proper classification. Eventually, the recognition of counterpart halves led to the discovery that the McIver fossils belong to the well known family Protasteridae. The unusual aboral appearance is due to the presence of a distinctive series of carinal spines. Further review of published descriptions of the Protasteridae led to discovery of similar series of carinal spines in *Strataster ohioensis* Kesling & Le Vasseur and *Drepanaster wrighti* Kesling. The importance of this morphology to the analysis

of the origin of ophiuroid upper arm plates and to the general question of homologies between the crinoid arm and the somasteroid ray is the topic of the general part of this paper. The first part concerns the systematic paleontology of the genus *Strataster* Kesling & Le Vasseur, and the description of *S. maciverorum*.

#### Systematic Paleontology

*Note on methods.*—The McIver fossils are preserved as molds and were studied from rubber casts, utilizing either latex or silicone rubber. The “disc radius” ( $r$ ) and “arm length” ( $R$ ) were measured from the center of the disc. [Because many Paleozoic ophiuroids do not have a well defined circular disc and have the general outline of a slender armed starfish, W. K. Spencer (1934:464, 468) established the practice of reporting disc radius, rather than disc diameter, for measurements on Protasteridae.] The

“width of the arm” (w) is measured at the edge of the disc and does not include the width of the splayed arm spines.

The material has been closely examined for evidence of Lovén's law by recording the arrangement of the ambulacral plates (Hotchkiss 1978). Examined from the oral surface, the ambulacral series on the anti-clockwise side of each arm is either in advance (A) or behind (B) the series on the clockwise side of the arm. Data are recorded as if each specimen presents an oral aspect. The arrangement AABAB is Lovénian. If the madreporite is not identified, data are recorded only if it is possible to determine which column is ahead of the other for at least four of the five arms. If the madreporite is identified on the specimen, the madreporic interradius is designated interradius III/IV and the labels I, II, III, IV, V are applied to the arms. Data are recorded for each scorable arm (even if only one arm can be scored).

The material has been closely examined for evidence bearing on the question of orientation to substrate (cf. Schuchert 1915: 30, 1919:6, 7; Fell 1963:429, 430; Smith & Jell 1990:766, 775, fig. 53) and for other aspects of behavior in life.

Class Ophiuroidea Gray, 1840

Order Oegophiurida Matsumoto, 1915

Suborder Lysophiurina Gregory, 1897

Family Protasteridae S. A. Miller, 1889

*Strataster* Kesling & Le Vasseur, 1971

*Strataster* Kesling & Le Vasseur, 1971:305, 317.—Kesling, 1972:10 in part (*S. ohioensis* but not *S. devonicus*).—Hammann & Schmincke, 1986:61.

*Drepanaster*.—Kesling, 1970:74 in part (*D. wrighti* but not *D. scabrosus*, *D. grayae*, and *D. schohariae*). [Not *Drepanaster* Whidborne, 1898]

*Eugasterella*.—Harper, 1985:361, 363 in part (*E. ohioensis* but not *E. logani* and *E. devonicus*). [Not *Eugasterella* Schuchert, 1914]

“new genus”.—McIver & McIver, 1955:159.

*Type species*.—*Strataster ohioensis* Kesling & Le Vasseur by original designation.

*Diagnosis (amended herein)*.—Protasterid brittlestars with upper arm plates and carinal spines; upper arm plates are not in register with the ambulacrals, and their series end before the arm tip. Uppermost vertical spines project at a high angle from the sides of the arms. Aboral outline of proximal ambulacrals trapezoidal, accommodating large dorsal longitudinal muscles. Disc radius up to 8 mm; arm length five to six times disc radius. Where arms become free of disc, their width (not including splayed vertical spines) equals about half the disc radius.

*Included species*.—*Strataster ohioensis* Kesling & Le Vasseur, 1971, type species; *Strataster wrighti* (Kesling, 1970) new combination; *Strataster maciverorum*, new species; not *Strataster devonicus* Kesling, 1972, referred to *Eugasterella* by Harper (1985).

*Remarks*.—No other known genera share the full set of characters in the revised diagnosis. In particular, no others are known to have carinal spines. Hamling's Ophiuroid has upper arm plates, but it lacks carinal and disc spines (Hotchkiss 1980). The splayed uppermost vertical spines and their contribution to the overall appearance of the arm is not known in any other genus.

Harper (1985:363) regarded *Strataster* as a subjective synonym of *Eugasterella* Schuchert, 1914, which has proximal ambulacrals deeply excavated for insertion of dorsal longitudinal muscles. I accept Harper's new combination *Eugasterella devonicus* for *Strataster devonicus*, but *Eugasterella* does not have carinal spines and upper arm plates, and it is necessary to retain *Strataster* as a distinct genus.

The arrangement of the ambulacral plates of all three species conforms with Lovén's Law for echinoids (see, e.g., Melville & Durham 1966:U221–U222). The hypothesis that the ophiuroid madreporite is located in

interradius III/IV (Hotchkiss 1978) is supported by the new *Strataster* data.

About half the specimens on a slab of rock are preserved with the oral side up, the others with the oral side down. The carinal spines of *Strataster* are similar to those of modern starfish such as *Calliaster*, *Oreaster* and *Asteropsis*, all of which have the usual eleutherozoan orientation of mouth and ambulacra in contact with the substrate. The orientation of *Strataster* in life is inferred by the presence of carinal spines, to be "oral side down."

As *Strataster* has upper arm plates, a revised diagnosis of the Oegophiurida is required. The origin of ophiuroid upper arm plates is discussed below in the general part of this paper.

*Strataster ohioensis*

Kesling & Le Vasseur, 1971

*Strataster ohioensis* Kesling & Le Vasseur, 1971:305, 317, pls. 1–13.—Halpern, 1972:8.—Kesling, 1972:10.—Hotchkiss, 1978:542.—Hotchkiss, 1980:93.

*Eugasterella ohioensis*.—Harper, 1985:369, 371.

*Diagnosis*.—Carinal spines begin near the periphery of the disc; there are approximately 13 spines in the space of four ambulacrals. The carinal spines are not preserved in a rigid erect position; instead they are recumbent, usually all leaning in the same direction, and certainly not fused to the upper arm plates. The splay of the uppermost vertical spines nearly doubles the overall arm width so that it nearly equals the disc radius. The disc tends to have convex interradii, lacks spines, and is covered above and below by minute granules which conceal underlying plates. [Partly based on Kesling & Le Vasseur, pl. 7, fig. 2.]

*Types*.—Type-bearing slabs in the University of Michigan Museum of Paleontology and in the collection of Le Vasseur are listed by Kesling & Le Vasseur (p. 330). The

caption to their plate 4, figure 2, designates UMMP 58329a as the holotype.

*Lovén's Law*.—The remarkable preservation of the specimens, and the clarity and scale of the photographs, allow investigating whether Lovén's Law applies to *S. ohioensis*. Three specimens have four or five arms that can be scored in oral view, and the madreporite is not identified on the photographs:

Paratype L-25a	A	A	B	A	?
Paratype L-25f	A	A	B	A	B
Paratype L-25h	A	A	B	A	B

Three specimens have arms that can be scored in oral view and the madreporite (\*) is identified on the photographs:

	I	II	III	*	IV	V
Paratype UMMP						
58332a	A	A	B	*	A	B
Paratype L-25e	A	?	B	*	A	B
Paratype L-25i	?	A	?	*	?	?

These data indicate that Lovén's Law applies to *S. ohioensis* and that the madreporite is located in interradius III/IV.

*Orientation and behavior*.—Kesling & Le Vasseur (p. 338) inferred that *S. ohioensis* was a filter feeder and could hold nearly the full length of the arms vertical while holding onto the substrate with the proximal tube feet near the mouth. They hypothesized that the crest of closely spaced carinal spines may have been used to pull surface silt over the brittle star's body and arms (negative phototactic response). About half of the specimens were buried with the oral side up and the others with the aboral side up (p. 330), and Kesling & Le Vasseur suggested that currents overturned the animals before burial (pp. 338, 339).

*Remarks*.—Many authors refer to the paper by Kesling & Le Vasseur (1971) on *S. ohioensis* when discussing ophiuroid communities, population densities, arm regeneration frequency, and the fossil record of brittlestar beds (Meyer 1984; Aronson & Harms 1985; Aronson 1987; Aronson &

Sues 1987, 1988; Meyer 1988; Aronson 1989, 1992). The size range is from about 1.2 mm disc radius to about 4 mm disc radius. Weathered specimens show that the proximal ambulacrals are trapezoidal in aboral outline, leaving large spaces for dorsal longitudinal muscles. The arrangement of the carinal spines suggests that in life they may have been interconnected by a web. Kesling & Le Vasseur report (p. 318) that each spine articulates by a ball-and-socket joint, precisely like the spine of an echinoid; also, where spines are missing, the tubercles on which they articulated are conspicuous because they are larger than the papillae, and are surrounded by a circular groove.

*Age and locality.*—Early Mississippian, Meadville Shale. Vicinity of Cleveland, Cuyahoga County, Ohio.

*Strataster wrighti* (Kesling, 1970),  
new combination

*Drepanaster wrighti* Kesling, 1970:75, pls. 1–2.—Hotchkiss, 1978:542.—Hotchkiss, 1980:93.

*Diagnosis.*—Carinal spines (inferred from sockets) begin their series midway between center and edge of disc, extend onto the arms, and number about five in the space of four ambulacrals (based on Kesling's plate 2, figure 1). The carinal spines are not erect, and are not fused to the upper arm plates. The splay of the uppermost vertical spines nearly doubles the overall arm width so that it nearly equals the disc radius. Aboral surface of disc ornamented with granules and with few scattered spines (presence inferred from sockets). Oral interradial with numerous spines.

*Types.*—The holotype and only specimen known is in the University of Michigan Museum of Paleontology, UMMP 57497.

*Lovén's Law.*—The holotype has five arms scorable in oral view (Kesling 1970:pl. 2, fig. 3), and the madreporite is not discernible (p. 75). The specimen obeys Lovén's Law:

Holotype UMMP

57497

A A B A B

*Remarks.*—The disc radius of about 2.7 mm is in the middle of the size range for *S. ohioensis*. The count of about five carinal spines in the space of four ambulacrals is distinctly different from the count of 13 in four in *S. ohioensis*. It agrees with *S. ohioensis* in the obviously loose attachment of its carinal spines. In fact, the spines are not found on the holotype, but their former presence is shown by a line of vacant sockets which Kesling (p. 75) described as "pustular bases for attachment of spines," and which he noted extend from the aboral surface of the disc [Note: typographical error in his text says "oral surface"] onto the aboral proximal part of the arms. The spine sockets confirm the presence of upper arm plates. The count of five carinal spines in the space of four ambulacrals is probably not reliably different from the count in the new species to be described next. The disc outline of the holotype has generally concave interradial. The oral interradial spines are 0.3 to 0.4 mm long. The shape of the aboral surface of the proximal ambulacrals is hidden by upper arm plates and granules (presumably the shape is trapezoidal, as in *S. ohioensis*).

*Age and locality.*—Middle Devonian, Arkona Shale. Vicinity of Arkona, Middlesex County, Ontario, Canada.

*Strataster maciverorum*, new species  
Figs. 1–5

"new genus and species," McIver & McIver, 1955:159. *Strataster*, n. sp. Hotchkiss, 1976:12.

*Protaster logani.*—McIver & McIver, 1955:159. [Not *Protaster logani* (Hall, 1868)]

*Diagnosis.*—Carinal spines begin their series at or near the center of the disc and number approximately 13 in the space of eight ambulacrals. The carinal spines are preserved in a rigid erect position and are probably fused to the upper arm plates.

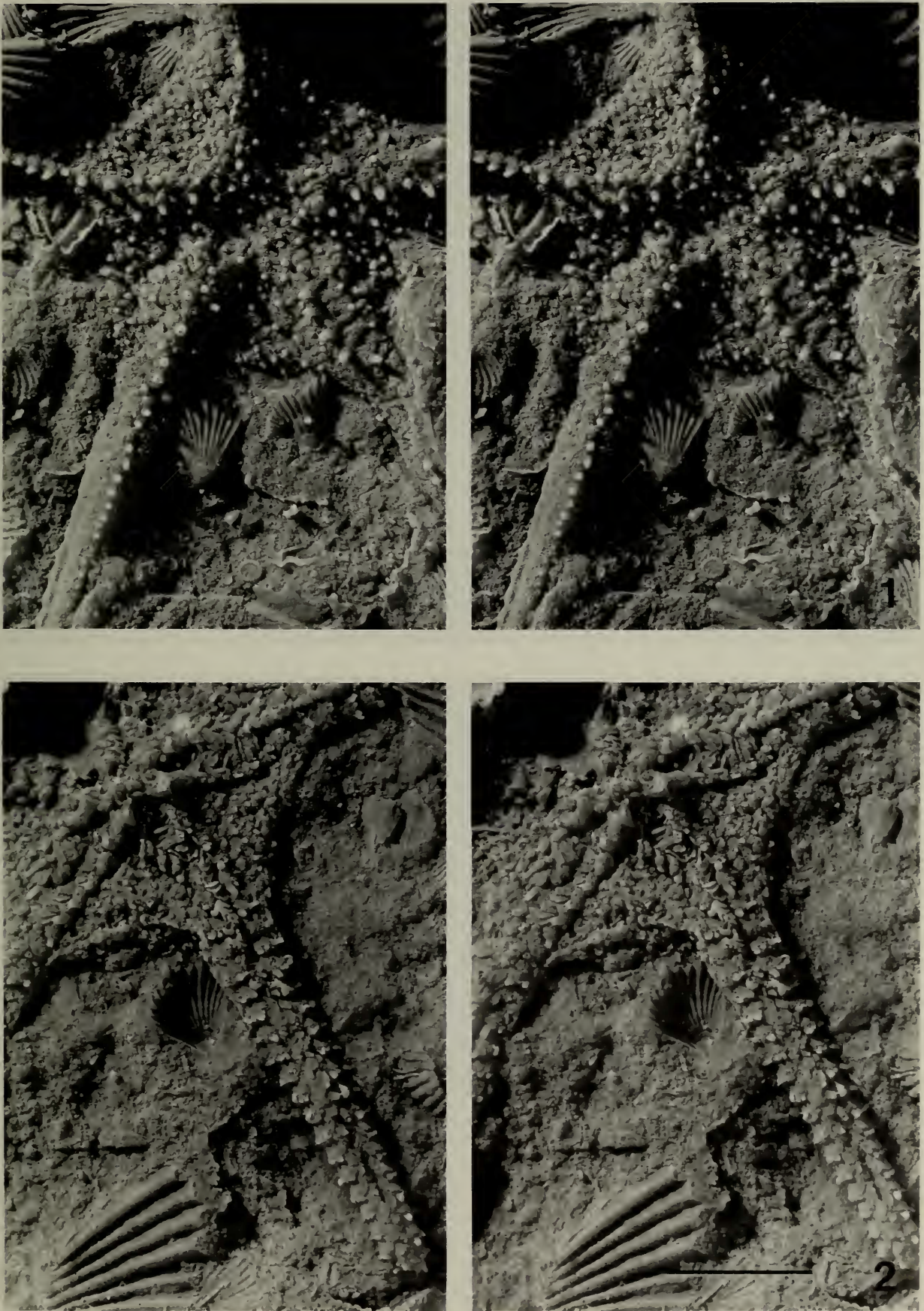


Fig. 1. *Strataster maciverorum*, new species. NYSM 13222, Holotype. Figured by McIver & McIver (1955). Counterpart halves. Latex pulls. Bar represents 5 mm and applies to both stereopair figures. 1.1, Aboral view. Carinal spines are preserved in a rigidly erect position, probably indicating fusion with the upper arm plates. Madreporic interradius at lower left. 1.2, Oral view. Groove spines completely close over the ambulacral groove on the oral surface. Madreporic interradius at lower right.



Fig. 2. *Strataster maciverorum*, new species. 2.1, NYSM 13225, Paratype. Aboral view. Carinal spines number approximately 13 in the space of eight laterals. Uppermost vertical spine short, splayed at a high angle to the arm axis. Latex pull. Bar represents 2 mm. For less enlargement see Fig. 3.1. For counterpart see Fig. 3.2. 2.2, NYSM 13223, Paratype. Aboral view. Carinal spines diminish in height distally. Latex pull. Bar represents 4 mm.



Fig. 3. *Strataster maciverorum*, new species. NYSM 13225, Paratype. Counterpart halves. Latex pulls. 3.1, Aboral view. Alternating ambulacrals visible through integument near arm tip at left. Madreporic interradius at lower right. Bar represents 4 mm. For greater enlargement see Fig. 2.1. 3.2, Oral view. Madreporic interradius at lower right. Bar represents 2 mm.



Fig. 4. *Strataster maciverorum*, new species. NYSM 13226, Paratype. Counterpart halves. Latex pulls. Bars represent 2 mm. 4.1, Aboral view. Most spines are missing; spine sockets locate their former positions. The few spines present are rigidly erect; evidently fusion of spine to plate is not complete. 4.2, Oral view. Note groove spines on arm at right.





Fig. 5. *Strataster maciverorum*, new species. NYSM 13224, Paratype. Latex pull. Bars represent 2 mm. Aboral views. Disc radius ( $r$ ) 7.5 mm. The disc surface is impressed onto the mouth frame. Note the plump cylindrical arms. Carinal spines evident, but less distinct than in smaller specimens.

Table 1.—Measurements of *Strataster maciverorum*, new species. NYSM, New York State Museum catalog number; r, disc radius; R, distance from center of disc to the arm tip; w, width of arm at edge of disc (does not include the width of the splayed arm spines); DS, rock specimen number.

NYSM	r	R	w	R:r	w:r	Remarks
13222	5.5 mm	34 mm	2.5 mm	6:1	1:2.2	holotype; DS17
13223	8	26+	4.5	—	1:1.8	paratype; DS9
13224	7.5	29+	4	—	1:1.9	paratype; DS37
13225	5	24	2.5	5:1	1:2.0	paratype; DS11, DS24
13226	4.5	15+	2	—	1:2.3	paratype; DS11, DS24

Similar plates and spines occupy the rest of the aboral surface of the disc, diminish in size toward the interradial margins, and are smaller still on the oral interradia. Splayed uppermost vertical spines are very short, less than half the length of an arm segment and do not materially contribute to the overall width of the arm. Interradial outline of disc tends to be concave.

*Types.*—There are six type-bearing pieces of rock, numbered DS9, DS11, DS17, DS17a, DS24, and DS37, collected by McIver and McIver and given to the New York State Museum (NYSM). DS11 and DS24 are counterpart halves of a single piece of rock, as are DS17 and DS17a. The single brittlestar (Fig. 1.1, 1.2) contained in rock specimen DS17 and counterpart DS17a is now catalogued as NYSM 13222; it was illustrated by the McIvers and is designated the holotype of *Strataster maciverorum*. There are four paratypes: one each in DS9 (Fig. 2.2) and DS37 (Fig. 5.1, 5.2), now catalogued as NYSM 13223 and NYSM 13224, respectively, and two in DS11 and counterpart DS24. Of the latter two, one is oral side up and one is oral side down: NYSM 13225 refers to the individual (Figs. 2.1, 3.1, 3.2) preserved as an aboral impression in rock specimen DS11, and NYSM 13226 refers to the individual (Fig. 4.1, 4.2) preserved as an aboral impression in rock specimen DS24.

*Additional material.*—The asteroids and ophiuroids found by the McIvers were identified by Prof. John W. Wells of Cornell

University, who pointed out that the specimens may belong in a new genus and species. Labels show that the “*Protaster logani*” of the McIvers’ article are contained in rock specimens DS1, DS2 (figured by the McIvers), DS3, DS12, DS18, DS25, DS30, DS70, and DS75. These rocks contain impressions of the oral surface of a protasterid brittlestar that resembles *Eugasterella logani* (Hall), the single type specimen of which is itself an impression of the oral surface without counterpart. These specimens are most likely oral impressions of *S. maciverorum*, an inference based on the observations (1) that the specimens which Prof. Wells distinguished as a new generic type are in every case impressions of the aboral surface, and (2) that counterpart impressions of these last are indistinguishable from the oral impressions that do not have counterparts. Hence these specimens are identified here as topotypes of *S. maciverorum*. Remains of *Devonaster* are present in rock specimens DS3, DS4, DS19 and DS24; remains of *Encrinaster* sp. are present in DS23.

*Etymology.*—The species is named in memory of Dr. Monroe A. McIver and Elizabeth P. McIver of Cooperstown, New York, who donated these prize fossils to science. [According to ICZN Code Recommendation 21a (1985), the prefixes “Mac,” “Mc” or “M” should be spelled “mac,” hence “*maciverorum*”; I thank Dr. David L. Pawson for pointing this out to me.]

*Measurements.*—See Table 1.

*Lovén’s Law.*—Two impressions of the

oral surface have a recognizable madreporite together with one or more arms that are scorable.

	I	II	III	*	IV	V
Topotype DS12	A	A	?	*	A	B
Topotype DS70	?	?	B	*	?	?

The data indicate that Lovén's Law applies to *S. maciverorum* and that the madreporite is located in interradius III/IV.

*Orientation and behavior.*—The carinal spines and plates of *S. maciverorum* are very asteroid-like, and suggest that the orientation in life was with the oral side toward the substrate. Paratypes NYSM 13225 and 13226 that are preserved on the same piece of rock (DS-11) but in opposite orientation to each other probably indicate some sort of turbulence at the time of burial.

The fossils show that *S. maciverorum*, together with the starfish *Devonaster eucharis*, lived on a muddy bottom with brachiopod and pelecypod shell life and shell rubble as part of the benthic epifauna (for faunal lists see Rickard & Zenger 1964). Crevice seeking behavior may be recorded by the ophiuroid in rock specimen DS-2 which has its aboral surface pressed against the inside (concave) surface of a clam shell (the mold is of course convex). As noted by Parsley (1981:K2) for specimens of the Ordovician stylophoran *Enopleura* that seem to have taken refuge under brachiopod shells, the position of the specimen seems "to be deliberate, rather than being the result of fortuitous preservation." Berry (1939) reached similar conclusions concerning finding numerous well preserved specimens of the Miocene *Ophiura marylandica* inside the shells of the large gastropod *Fulgar coronatum*.

The very straight arms of the holotype (Fig. 1.1, 1.2) may be the result of a stiffening reaction such as occurs in many living ophiuroids in response to being disturbed. This reaction is attributed by Byrne & Hen-

dlar (1988) to catch connective tissue which Motokawa (1988) believes was also present in Paleozoic echinoderms. Byrne & Hendler (1988) also propose that Paleozoic ophiuroids with limited arm mobility but large podial basins may have been vagile members of the epifauna, walking around on the tips of large tube feet, a suggestion based on observing *Ophiogeron supinus* from the *Johnson-Sea-Link* submersible.

*Remarks.*—All five specimens of *S. maciverorum* are larger than the largest of the 100 *S. ohioensis* that were measured by Kesling & Le Vasseur (1971). The largest *S. maciverorum* (NYSM 13223, Fig. 2.2) is twice the size of the largest *S. ohioensis*. As in *S. wrighti*, the shape of the aboral surface of the proximal ambulacrals of *S. maciverorum* is hidden by the upper arm plates and granules.

The considerable differences between *S. maciverorum* and *S. ohioensis* are partly bridged by *S. wrighti*. *S. ohioensis* has loosely articulated crowded carinal spines and no disc spines. *S. maciverorum* has rigid uncrowded carinal spines and many such spines on the disc. *S. wrighti* bridges the gap by having loosely articulated uncrowded spines and a few such spines on the disc (inferred from spine sockets on the disc and arms).

The distinguishing marks of *Strataster* and its species are found on the aboral surface. The same is true of many other Protasteridae, which makes it difficult to identify a protasterid for which only an oral view is available.

What is the function of the upper arm plates and carinal spines? It is known (Hendler & Byrne 1987) that ophiuroid upper arm plates may contain structures that focus light onto photoreceptor cells. It is likely that the upper arm plates and carinal spines of *Strataster* provided it with a degree of protection from predation. This would be especially valuable if *Strataster* had gonads in the arms, as surmised for the Oegophiurida by Fell (1963) and Petr (1988), because

the loss of an arm then also represents the loss of reproduction potential.

*Age and locality.*—Middle Devonian (Erian Series), Panther Mountain Formation. Vicinity of Cooperstown, Otsego County, New York. From a road cut (McIver & McIver 1955:photograph) on N.Y. Route 28, 1.7 miles west of Cooperstown in the Cooperstown Quadrangle. Designated New York State Museum Paleozoic Fossil Locality 6428. For a geologic map and treatment of the stratigraphy of the quadrangle, see Rickard & Zenger (1964).

#### Discussion of Ophiuroid Upper arm Plates

The present account, and a previous paper on the early growth stage represented by Hamling's Ophiuroid (Hotchkiss 1980) are the first to demonstrate the presence of upper arm plates in members of the brittlestar order Oegophiurida. [Salter (1857:323) thought that *Lapworthura miltoni* (Salter) had a double series of upper arm plates, but Sollas & Sollas (1912:217) showed that the upper surfaces of the ambulacral vertebrae merely create the impression of a double row of upper arm plates and that upper arm plates are absent.] The new data allow further discussion of the history of the upper arm plates of modern ophiuroids.

*Ontogeny.*—Studies on living brittlestars (e.g., Clark 1914) have shown that upper arm plates are the last plates laid down in an arm segment, and that arm segments are always added at the arm tip. The upper arm plates of the species of *Strataster* do not extend to the distal (younger) parts of the arms, and this is proof that here too they are the last plates of an arm region to be laid down. It can therefore be said that not only are there more plate systems in common between ancient and modern ophiuroids than has previously been recognized, but also that there is agreement in the sequence in which the plates are laid down.

Fewkes suggested a century ago (1887:145) that the absence of upper arm plates in

*Ophiohelus* (moved from the Ophiacanthidae to the Ophiomyxidae by Spencer & Wright 1966:U89), *Ophiambix* (Ophiacanthidae), and *Astrophyton* (Gorgonocephalidae) could be "due to degradation, or the genera have not progressed through embryonic stages in which dorsals appear, if, as is probably the case, dorsals have never appeared." Mortensen (1913) showed that the upper arm plates in the alleged primitive ophiuroid *Ophioteropsis elegans* Bell [shown by Mortensen to be *Ophiothela tigris* Lyman] are being formed at the arm tip but are being resorbed while still of microscopic size. These possibilities offer a plausible explanation for the lack of upper arm plates in most of the previously described Oegophiurida and Stenurida.

*Morphology.*—Upper arm plates in the genus *Strataster* differ radically from those of extant ophiuroids and closely resemble carinals of starfish.

Relation to the axial arm skeleton: Upper arm plates of extant ophiuroids are perfectly correlated with the arm segmentation of the free portion of the arm, there being one upper arm plate to each segment. In *Strataster* the halves of ambulacral vertebrae are not in pairs simulating vertebrae, and so there is no arm segmentation comparable to that of extant ophiuroids. Even so, the upper arm plates of the species of *Strataster* might be expected to show serial correlation with the ambulacrals, but such is not the case. In *S. ohioensis* there are approximately 13 upper arm plates in the space of four ambulacrals, and in *S. maciverorum* approximately 13 upper arm plates occur in the space of eight ambulacrals. Thus there is no one-to-one serial correlation between upper arm plates and ambulacrals in these lysophiurine oegophiurids. Nor is there one-to-one correlation between asteroid carinals and the ambulacrals of the asteroid arm.

Spines: Upper arm plates of extant ophiuroids lack carinal spines. [Note: Some extant ophiuroids do have granules or spinules attached to or surrounding one or more upper arm plates, but, as commented by a re-

viewer, “they are not articulated and therefore not homologous with protasterid carinal spines”; for examples see Clark 1911:figs. 38, 43–49, 100, 101, 106, 126, 131, 134.] In contrast, carinal spines are a highly conspicuous feature in *S. ohioensis* and *S. maciverorum*. The carinal spines of *S. maciverorum*, particularly, are very “asteroid-like.” These spines almost certainly indicate that these animals lived with their oral side down as in modern sea stars.

Relation to the aboral disc skeleton: Embryologists (e.g., Murakami 1941:73) have found that upper arm plates of Ophiurida begin their series with the first arm segment (the third if elements of the mouth frame are counted). As the animal grows, the upper arm plates associated with those arm segments that become included in the disc region are displaced and crowded together at the place where the arm becomes free of the disc (Berry 1934:73, fig. 9). In *S. maciverorum* and *S. wrighti*, however, the upper arm plates begin their series well within the disc region, an arrangement exactly comparable to that seen in asteroids.

*Homologies.*—Examination of the homologies of upper arm plates necessitate a brief excursion into the homologies of other plates as well. A summary of the revised homologies is given in Tables 2 and 3.

Homologies of brachials and upper arm plates: Carpenter (1887:309, footnote) concluded that the brachials of a crinoid are in a general way represented in the ophiuroid by the upper arm plates. Sladen (1884:30) shared this view and applied the term “brachial” to the median dorsal line of plates of the starfish ray as seen in juvenile *Zoroaster fulgens*. Fell (1963:414), however, concluded that the carinal plates of asteroids, and the dorsal arm plates of ophiuroids, are late structures, not homologous with any brachial ossicles in crinoids. According to Fell (pp. 419, 420) the brachial ossicles of crinoids are homologous with the ambulacral ossicles of asteroids and ophiuroids, not with dorsal arm plates or carinals. The discovery of upper arm plates in *Strataster*, Hamling’s

ophiuroid, and *Rhopalocoma* led Hotchkiss (1974) to accept the views of Carpenter and Sladen over that of Fell. It is shown below, however, that Fell’s homology of brachials with ambulacrals is correct, and that upper arm plates are not represented in crinoids.

Homologies of radial shields and upper arm plates: Fewkes (1887:130) believed that ophiuroid radial shields are homologous with the first paired brachials of crinoids. This view was discredited by Carpenter (1887:308–309) based on study of crinoids.

Fell (1963:420) argued that radial shields are a late phylogenetic development and are not part of the calyx: “Their development in Euryalina shows that they arise from an adradial series of platelets equal in number and position to those segments of the arm which have been incorporated into the disc below. Thus they are homologous with the dorsal arm-plates of the rest of the radius; as indeed their arrangement in many ophiuroids suggests, for the basal dorsal arm-plates are often split into two portions, right and left.” This interpretation, however, does not accord with the observations of Lyman (1882) concerning the development of radial shields or with the fate of the first few upper arm plates in genera such as *Ophier-nus*.

Lyman (1882:157) examined minute young of *Hemipholis elongata* [as *H. cordifera*] and concluded that “radial shields, so nearly universal among ophiurans, are not special plates, but entirely homologous with other disc scales, and by no means the first to appear.” He showed (p. 271, pl. 44, figs. 10, 11, *l*) that in *Astrogomphus vallatus* the radial shields “are made up of several overlapping pieces soldered together.” He described (p. 167) the genus *Ophiocoma* as having radial shields that “are continued inward [toward the center of the disc] by a broad stripe of large, strongly overlapping scales, a feature nowhere so developed as in this genus.” His descriptions and figures show that the platelets referred to by Fell greatly exceed the number of arm segments in the disc, and that the accretion of platelets

Table 2.—Revised homologies of plates of the aboral surface (tissues derived at metamorphosis from the right side of the larva).

Asteroids	Ophiuroids	Crinoids
Primary circlet:		
centrale	centrale	terminal stem plate (attachment disc) of comatulid larval stalk
primary interradials [cf. <i>Zoroaster</i> ]	primary interradials	? topmost stem pentameres [cf. <i>Aethocrinus</i> ]
primary radials	primary radials	? infrabasals
carinal plates [=serial homologues of primary radials]	upper arm plates [=serial homologues of primary radials]	—(absent)
Extraxial skeleton:		
the aboral skeleton outside the circlet of primary radials [superomarginals are differentiated members of the aboral extraxial skeleton]	the aboral skeleton outside the circlet of primary radials [the radial shields of advanced ophiuroids are modified aboral disc plates]	the aboral skeleton [=basals] outside the circlet of infrabasals

is toward the center of the disc (whereas upper arm plates develop in succession distally). [I thank a reviewer for the following additional information: “It is incorrect to infer from Lyman’s illustrations that radial shields grow by adding platelets proximally. Each of the plates arises from a single spicule and growth proceeds by the enlargement of an ossicle—not by the incorporation of additional ossicles. However, this does not invalidate the suggestion that they are disc scales.”]

In *Ophiernus*, which has been very well described by Madsen (1977), the upper arm plates that correspond to those segments of the arm which have been incorporated into the disc certainly do not go into the making of radial shields. Instead, they accumulate at the edge of the disc. As a consequence they are no longer associated with their proper arm segments, and so we find examples of the first six proximal arm plates partially resorbed and compressed into the space of just three arm segments. Observations by A. M. Clark (1974:443 [fig. 1], p.462 [fig. 10a]) show that the upper arm

plates of *Amphilimna cribriformis* and *Ophionephthys lowelli* do not contribute to the making of radial shields; in the latter instance, upper arm plates that are overgrown by the disc are found to be divided by “erosion of the median part” into left and right halves that are presumably on their way to being completely resorbed.

The upper arm plates of all three species of *Strataster*, Hamling’s Ophiuroid, and *Rhopalacoma*, are entire, not split in two to form a double row. Upper arm plates arise ontogenetically from a single center of calcification (e.g., Murakami 1940:32). The two (and sometimes more) pieces of upper arm plates found in some extant ophiuroids must be the result of fragmentation of an initially entire plate (Lyman 1882:20), or are evidence for the existence of additional plates lateral to the true upper arm plates. In fact, both median and lateral upper arm plates were demonstrated in “*Ophioteropsis elegans*” by Mortensen (1913:8). Similar “fragmented” plates were described in *Ophiomyxa*, *Ophiobyrssa* and *Ophiogeron* by Byrne & Hendler (1988). Thus, the sup-

Table 3.—Revised homologies of plates of the oral surface (tissues derived at metamorphosis from the left side of the larva).

Asteroids	Ophiuroids	Crinoids
Axial skeleton:		
ambulacral plates [evolved from stromatocystitid biserial flooring plates] terminal (ocular) plates	ambulacral plates + sublateral plates [sublateral plates are part of the ambulacral series in <i>Rhopalocoma</i> ] terminal (ocular) plates	brachial plates [radials = 1st plates of brachial series] [pinnules = heterotomous arm branching] —(absent)
Adaxial skeleton:		
adambulacral ossicles [evolved from stromatocystitid primary cover plates] adaxial virgalia [evolved from stromatocystitid cover plate series] [=asteropseid growth gradient metapinnules]	lateral arm plates [mouth angle plates of jaw]  adaxial virgalia [pinnate 3rd virgal reported in <i>Trichaster</i> , <i>Asteronyx</i> and <i>Astrophyton</i> by Fell (1963)]	—(absent)  —(absent)
Admarginal skeleton:		
admarginal virgalia [=poraniid growth gradient metapinnules] [=developmental homologues of inferomarginals]	—(unknown)	—(absent)
Marginal skeleton:		
inferomarginal ossicles [homologous with the stromatocystitid marginal frame]	[cf. marginalia in <i>Rhopalocoma</i> ]	—(absent)

posed homology between radial shields and upper arm plates is not supported by either embryology or the new fossil evidence.

Homologies of the calycinal plates of ophiuroids and crinoids: Carpenter (1884), Sladen (1884), Fell (1963), and Hotchkiss (1974, 1980) believed that the primary radial plates of ophiuroids and asteroids are homologous with the radial plates of crinoids. This turns out to be a major source of misdirection in inferring correct echinoderm plate homologies. If in crinoids the brachials are serially homologous with the radial plate, then where are the serial homologues of the primary radial plate in the Asterozoa? For Carpenter (1887:309, foot-

note) the answer lay with the ophiuroid upper arm plates. For Fell (p. 419) it lay with "asterozoan" ambulacral plates. To relocate "asterozoan" ambulacral plates from the aboral surface (where the calycinal system develops) to the oral surface (where ambulacrals are part of the jaw apparatus), Fell postulated a "dislocation of the main radial growth gradient at the junction of the radial calycinal plate and the first brachial ossicle" (p. 382). This is Fell's mechanism for the evolution of the Asterozoa from a crinoid-like ancestor. Although Fell (p. 414) states that evidence of a dislocation is directly observable in the ontogeny of Recent Asterozoa, this is contradicted by the fact that pri-

mary radials develop in tissues derived from the right side of the bilateral larva whereas the ambulacrals develop in tissues derived from the left side (Sladen 1884:37, Murakami 1937:137, figs. 3–5).

As pointed out recently by Broadhead (1988:255), Hyman (1955:57, 85, 698) broke away from this misdirection. In *Antedon*, rudiments of the radial plates are not present until the end of the cystidean stage. According to Hyman, the radial plates are “not true thecal or calycinal plates but the first plates of the brachial series.” This interpretation, which is accepted by Broadhead, means that the primary radial plates of ophiuroids cannot represent the radials of crinoids.

The idea that upper arm plates may be serially homologous with ophiuroid primary radials does not conflict with the idea that brachials are serially homologous with crinoid radial plates. The interpretation by Philip and Strimple (1971) of the Lower Ordovician archaic inadunate crinoid *Aethocrinus* leads me to consider that the primary radials of Hamling’s ophiuroid (Hotchkiss 1980) may be equivalent to the infrabasals of *Aethocrinus*. The primary interradials of developing Asteroidea lie inside the circlet of primary radials (Ludwig 1905:pl. 32, fig. 190, Blake 1990:347, 351); the corresponding circlet of ossicles in *Aethocrinus* are the topmost stem pentameres that in fact contribute to the theca. The centrale of ophiuroid early growth stages therefore seems to represent the terminal stem plate (attachment disc) found in the larval stalk of comatulid crinoids (a homology previously advocated by Carpenter 1878:374 and by Sladen 1884:35).

Homologies of the crinoid arm and the somasteroid ray: Fell (1963) saw in the structure of the somasteroid ray a pattern of skeletal growth gradients found elsewhere only among crinoids. Cover plates along the somasteroid metapinnules seemed to confirm the comparison with crinoid pinnules. He therefore considered somasteroid am-

bulacrals and virgalia homologous with crinoid brachials and pinnulars. Because there is no plate series in the crinoid arm that corresponds with ophiuroid upper arm plates, Fell interpreted the absence of upper arm plates in somasteroids and Paleozoic ophiuroids (Stenurida and Oegophiurida) as confirming evidence of his phylogenetic theory. But as shown here, upper arm plates were present in *Strataster*. Upper arm plates are not yet known from somasteroids, but it can now be supposed that they may have been present in at least the early growth stages. Thus the crinoid arm and the somasteroid ray do not appear to be comparable structures, and the comparisons and the homologies proposed by Fell are doubtful.

The ancestry of sea stars is now sought among the edrioasteroids. Detailed analysis of the marginal frame and the intermediate skeletons of sea stars (Hotchkiss 1974, Hotchkiss & Clark 1976) suggests homologizing the marginal frame of *Archegonaster* with the marginal frame of stromatocystitid edrioasteroids (Termier & Termier 1969, Smith & Jell 1990). According to Paul and Smith (1984:468) somasteroid ambulacrals are homologous with the primary ambulacral flooring plates of early Cambrian echinoderms; somasteroid virgalia are thought to be derived from stromatocystitid (*Cambraster*) cover plate series (p. 469). [The observation that crinoid pinnules arise from heterotomous arm branching (Paul & Smith 1984:466) whereas virgalia derive from edrioasteroid cover plate series is another reason that the crinoid arm should not be considered homologous with the somasteroid ray.] A search should be made for antecedents of upper arm plates in somasteroids and in stromatocystitid edrioasteroids.

Serial homology of primary radials and upper arm plates: That the upper arm plates of *S. maciverorum* and *S. wrighti* begin their series well within the disc region confirms the conclusion stated by Lyman (1882:270) that there is no distinction between the up-



per surface of the arms and that of the disc. Important to the present context, it shows that it is proper to compare upper arm plates with disc plates. Judging from *S. maciverorum* it is very likely that the plates that bear the first carinal spines are in fact the primary radial plates of the rosette (cf. Ludwig 1905:pl. 32, fig. 190). Hamling's ophiuroid and *Rhopalacoma pyrotechnica* (Salter) seem to answer unequivocally which disc plates hold the long sought homology. In both there is a direct serial relation and a virtually identical morphology between the upper arm plates and the primary radials. Upper arm plates are evidently fashioned after the plan prescribed by the genetic instructions for fashioning of primary radials, and therefore in every sense are serial homologues of the latter (cf. Hubbs 1944:293).

*Antiquity of upper arm plates.* — Wherever primary radial plates occur there is the potential for them to be serially repeated along each arm. Upper arm plates can therefore be as ancient as primary radials. The evidence from Hamling's Ophiuroid leads to the inference that primary radials are an inheritance from the somasteroid stem group ancestral to both asteroids and ophiuroids. It follows that upper arm plates were at least potentially, and perhaps were in fact, also present in stromatocystitid edrioasteroids.

The strong similarities between the upper arm plates of *Strataster* (also of *Rhopalacoma*) and the carinals of starfish can be stated as follows: Although the upper arm plates of modern ophiuroids lack the common asteroid character of bearing a carinal series of spines, and although asteroids lack the modern ophiuroid character of serial correspondence between upper arm plates and ambulacrals, these Paleozoic ophiuroids bridge both of these gaps. An obvious suggestion is that upper arm plates predate the divergence of the asteroid and ophiuroid lineages (the "asteroid/cryptosyringid divergence" of Smith 1988:88).

There is evidence for the antiquity of upper arm plates at every stage in the evo-

lution of the ophiuroid lineage. That the stenurid *Rhopalacoma* (perhaps also *Bdel-lacoma*) has upper arm plates could mean that upper arm plates predate the stenurid-oegophiurid divergence. That the protasterids *Strataster* and Hamling's Ophiuroid have upper arm plates could mean that upper arm plates predate the lysophiurine-zeugophiurine divergence. That certain phrynophiurids have upper arm plates could mean that upper arm plates predate the phrynophiurid-ophiurid divergence. That the Silurian *Argentinaster bodenbenderi* Ruedemann has typical upper arm plates (personal observation) may mean that upper arm plates date from the very beginning of at least the order Ophiurida.

Such statements are in complete disagreement with the conclusion of Ubaghs (1953:789) and Fell (1963:414) that upper arm plates developed late in ophiuroid phylogeny. They also depart from the conclusion of Sollas & Sollas (1912:218) that the late appearance of upper arm plates in ontogeny recapitulates a late phylogenetic history. Instead it appears that the developmental pathway for upper arm plates was present in the stem group ancestral to both asteroids and ophiuroids, and that the presence or absence of upper arm plates as a character state in Paleozoic ophiuroids was determined by genes that regulated expression of the pathway.

*History of upper arm plates.* — The history of ophiuroid upper arm plates therefore appears to be as follows. In the stem group ancestral to both asteroids and ophiuroids they were not in serial correspondence with the ambulacral series. This is quite understandable considering the plump arms of early asteroids and ophiuroids. This character state was carried over into stenurids and oegophiurids, where upper arm plates still lack serial correlation with the ambulacral skeleton. In the line of descent in which the ambulacrals of the two sides of the arms are staggered (Lysophiurina) perfect arm segmentation was an impossibility, al-

though remarkable arm flexibility was achieved. In the zeugophiurine oegophiurids, the ambulacrals of the two sides of the arm are in register, and arm segmentation was perfected when upper arm plates were brought into serial correspondence with the vertebrae. This condition is found among those phrynophiurids that express upper arm plates, and is well known among the Ophiurida.

This history requires that upper arm plates were present and exposed to natural selection in the somasteroid stem group ancestral to both asteroids and ophiuroids. Accordingly it is also necessary to explain the absence of upper arm plates among most of the previously described Paleozoic Oegophiurida and Stenurida. As in the case of explaining the lack of a primary rosette in post-juvenile Oegophiurida and Ophiomyxidae (Fell 1963:419), absence of upper arm plates in these fossils is best explained by resorption. Resorption of calcareous matter in ophiuroid growth series was noted by Clark (1911:3), and was documented for upper arm plates by Mortensen (1913).

#### Oegophiurida Rediagnosed

Matsumoto, the author of this order (1915:45, proposed as a subclass), included in his diagnosis the statement that upper arm plates are absent. Later authors have agreed with this statement (e.g., Spencer 1925:280, Fell 1963:407, Kesling 1970:74). On the basis of data provided by the species of *Strataster* and the specimens of Hamling's Ophiuroid, the diagnosis of the order must be amended, for these otherwise completely typical protasterid lysophiurine oegophiurids possess upper arm plates and carinal spines. As reported elsewhere (Hotchkiss 1980), Hamling's Ophiuroid shows that early growth stages of oegophiurids carry a centrale and primary radials. Accordingly, earlier generalizations based on presumed absence of these plates from oegophiurids must likewise be abandoned

(cf. Stürtz 1899:181–182; Spencer 1914:34–35, 1925:242–243; Philip 1965). Furthermore, it has only recently been discovered (Hotchkiss 1978) that Lovén's Law applies to Oegophiurida with alternating ambulacrals plates (Protasteridae and Encrinasteridae), and data are still being accumulated (Harper & Morris 1978:157, Harper 1985:367, herein). It therefore seems appropriate to conclude with a brief revised diagnosis of the order.

Oegophiurida are distinguished from Phrynophiurida and Ophiurida by a list of negative characteristics: ventral arm plates absent, bursae absent, genital plates and scales absent, radial shields absent, oral shields absent, adoral shields absent. Like phrynophiurids and ophiurids, some oegophiurids are now known to have upper arm plates, and early growth stages have been shown to have a centrale and primary radials. A more detailed report has explained that the extant *Ophiocanops* is not a living example of the Oegophiurida and that it is properly classified in the Phrynophiurida (Hotchkiss 1977).

Oegophiurida are distinguished from Stenurida by podial basins which are entirely on the distal portion of an ambulacral, by the absence of sublaterals, and by presence of no more than two fused ambulacral elements in the mouth frame. There are a few taxa classified as oegophiurids that have certain stenurid features, but their overall facies is that of a typical oegophiurid (e.g., *Protaster piltonensis* Spencer, and *Bundembachia benecki* Sturtz).

The suborder Lysophiurina obeys Lovén's Law (heretofore an echinoid trait). In the Lysophiurina the halves of ambulacral vertebrae are in offset series, whereas in the Zeugophiurina they are in register. Others have remarked before that the two lines of descent represented by these suborders effectively make the order polyphyletic (Ubaghs 1953:818). Provided that the limitations of the present classification are understood, there is no need to introduce any

broad changes into the classification until more work has been done on undescribed material in various existing collections.

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